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Editor's Preface

In the second issue of the 100th volume of the Journal of the Royal Society of Western Australia are obituaries of two prominent contributors to Western Australian natural science: geologist Philip E Playford (1931–2017) and environmental scientist Arthur J McComb (1936–2017). In addition there are two papers: on invasive fish species in the Perth metropolitan area, and the influence of fire on mosses, liverworts and lichen in southwestern jarrah forests.

A major symposium is planned for 27–28 July 2018 on 'Landscapes, Seascapes and Biota: Unique Western Australia—Past, Present and Future'. The symposium will present up-to-date reviews on many aspects of the natural sciences in Western Australia and will be highly relevant to those interested in disciplines ranging across the Biological, Earth, Marine, Environmental and Archaeological Sciences, as well as areas of Chemistry, Physics, Mathematics and Engineering applied to the natural sciences. The two-day conference will have 25 invited presentations and will also include posters on specific research topics. Manuscripts from the keynote talks will be published in the Journal.

In 2018 the submission and review process for articles to the Society is to be managed by Scholastica at https://rswa.scholasticahq.com/ where an updated guide to authors is available as well as the submission portal.

Arthur Mory

BHL

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Continued invasion: New detections of non-native freshwater fish in wetlands of the Swan Coastal Plain, Western Australia, and management recommendations

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Abstract

Introduced fishes are a major environmental problem worldwide and correlate with increasing human populations; this is not surprising as many introduced species originate from the ornamental trade and are released by hobbyists. The current survey of wetlands on the Swan Coastal Plain within the Perth metropolitan region detected three introduced species previously not recorded in the State: the long-finned eel *Anguilla reinhardtii* Steindachner 1867, the jaguar cichlid *Parachromis managuensis* (Günther 1867), and the southern platy *Xiphophorus maculatus* (Günther 1866). Whereas *X. maculatus* has established a self-sustaining population only single specimens of *A. reinhardtii* and *P. managuensis* were captured. The study highlights the importance of ongoing monitoring to facilitate early detection and eradication of introduced fishes, along with continued investment in public education to change behaviour that reduces the risk of further introductions of new species.

Keywords: Alien species, *Anguilla reinhardtii*, *Parachromis managuensis*, *Xiphophorus maculatus*, Southwestern Province, Swan Coastal Plain

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INTRODUCTION

Freshwater ecosystems worldwide have undergone rapid biodiversity loss (Dudgeon *et al.* 2006). In some freshwater systems rates of extinction have been calculated as up to five times higher than that for terrestrial faunas (Ricciardi & Rasmussen 1999). One of the largest impacts on freshwater systems, and a major cause of extinction in such environments, is the establishment of introduced fish species (Miller *et al.* 1989, Courtenay & Stauffer 1990, Richter et al. 1997, Sala 2000, Rahel 2002, Canonico *et al.* 2005, Dudgeon *et al.* 2006, Newman & Reantaso 2010). The rate of fish introductions is increasing (Courtenay & Stauffer 1990, Bunn & Arthington 2002, Lintermans 2010) with many resulting from the release of ornamental species sold in the aquarium trade (Courtenay & Robins 1973, Courtenay 1990, Courtenay & Stauffer 1990, Koehn & Mackenzie 2004). Within Western Australia, the majority of freshwater fish introductions originate from the ornamental sector (McKay 1984, Beatty & Morgan 2013).

Following introduction, several factors may determine whether the species establishes a self-sustaining population. These include: biological, physical and chemical properties of the waterbody; structure of the ecosystem; and the ecology of the species released (Moyle & Light 1996, Bomford 2008). Whereas not all release events result in self-sustaining populations, such instances are unlikely to be detected without active surveillance (see Duffy *et al.* 2013). Typically, it is only when a population of introduced fish becomes large, and/or causes an environmental impact, that the species is detected. By this time, it is often too late for eradication attempts as the chance of success is extremely low (Myers *et al.* 2000).

Wetlands in urban areas are at particular risk to the establishment of pest species. With increased population, not only do more people keep fish, but wetlands in urban areas are often highly modified, which can enhance the establishment of introduced species (Ross 1991, Gehrke *et al.* 1995, Walker *et al.* 1995, Moyle & Light 1996, Bunn & Arthington 2002, Rahel 2002). Within Western Australia, wetlands in the Swan Coastal Plain contain most of the State's introduced freshwater species (Beatty & Morgan 2013, Morgan *et al.* 2014) coincident with the highest human population in the State (Australian Bureau of Statistics 2011). Prior to the current survey, 13 introduced species were known from the Swan Coastal Plain, outnumbering the 11 native freshwater fishes from Australia's entire Southwestern Province (Morgan *et al.* 2004, Beatty & Morgan 2013, Duffy *et al.* 2013, Hourston *et al.* 2014, Morgan *et al.* 2014).

The Western Australian Department of Primary Industries and Regional Development actively educates the public on the risks of releasing unwanted aquarium fish into waterbodies, and has multiple avenues for the reporting of introduced fish sightings. A combination of recent field surveys (Duffy *et al.* 2013) and new reports of pest species has highlighted a lack of information on the distribution of introduced fish in waterbodies of the Perth metropolitan region. The lack of information hinders

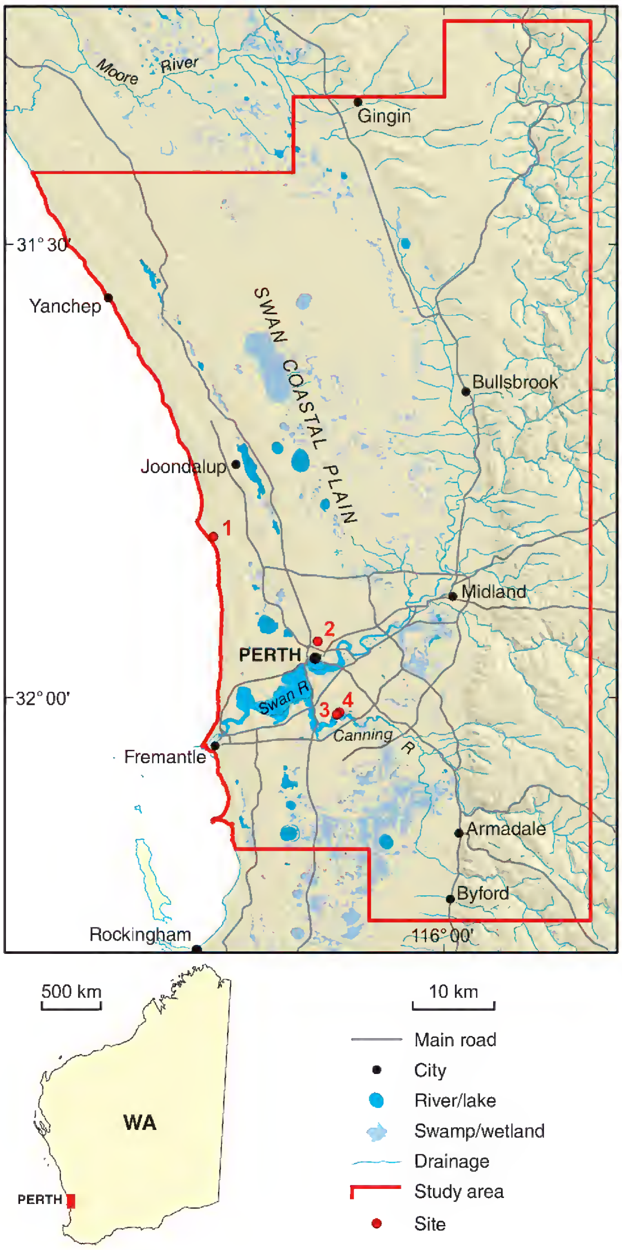

Figure 1. Study area containing waterbodies sampled and the location of new findings of: 1) *Anguilla reinhardtii*, Lacepede Park, Hillarys; 2) *Parachromis managuensis*, Hyde Park, North Perth; 3) & 4) *Xiphophorus maculatus*, Bodkin Park, Waterford and Sandon Park, Waterford, respectively.

informed decision making and the implementation of response actions. To address this, a comprehensive survey of metropolitan wetlands was undertaken. This paper describes the detection of three introduced species not previously recorded within Western Australia.

METHODS

A survey of fish assemblages in approximately 300 water bodies in the Perth metropolitan region was undertaken between January 2012 and January 2015. Fyke nets were utilised to sample water bodies; however, the particular specifications of the nets deployed depended on the physical characteristics of the water body. The net used most frequently was a D-mouth galaxid fyke (60 cm height) with a single 5 m wing made from 4 mm knotless woven mesh. In small or shallow water bodies smaller D-mouth galaxid fykes either 50 cm high with a 2.4 m wing or a 40 cm high with a 1.9 m wing were deployed. After the survey had commenced an additional large mesh (40 mm stretched) monofilament D-mouth fyke (60 cm height) with a 5 m wing was introduced to target larger species that may have avoided capture in the small meshed fykes.

The nets were deployed perpendicular to the bank. Where the size of the waterbody permitted, nets were set in a paired arrangement with an inner (closest to the bank) and an outer net by attaching the wing of the outer net to the cod end of the inner net. Nets were deployed from a kayak in the afternoon by 6 pm and were left overnight. To standardise soak time nets were retrieved the following morning from 7 am in the same order as deployment. The number of fyke nets deployed was dependent on the lake area and accessibility around its perimeter. DNA barcoding was used to confirm the identity of species not previously detected in Western Australia; the method is described in Duffy *et al* (2013).

RESULTS

Three species of fish not previously recorded in waterbodies in Western Australia were detected between January 2012 and January 2015: the long-finned eel *Anguilla reinhardtii* Steindachner, 1867, the jaguar cichlid *Parachromis managuensis* (Günther 1867), and the southern platy *Xiphophorus maculatus* (Günther 1866) (Table 1).

The two lakes in Bodkin Park next to the Canning River and their connecting channel containing *X. maculatus* were sampled on three occasions in winter,

Table 1. Newly detected species in the Perth metropolitan region. D = detected, but no evidence of juvenile recruitment or additional specimens in follow up sampling; E = established breeding populations.

Family	Species	Date of initial detection	Lat.	Lon.	Lake	Status
Anguillidae	*Anguilla reinhardtii*	25/9/14	-31.822376	115.745640	Lacepede Park, Hillarys	D
Cichlidae	*Parachromis managuensis*	8/1/2015	-31.937779	115.860806	Hyde Park, North Perth	D
Poeciliidae	*Xiphophorus maculatus*	5/6/2013	-32.015773	115.884579	Bodkin Park, Waterford	E
		5/6/2013	-32.018354	115.881834	Sandon Park, Waterford	E

summer and spring. The lowest abundance was in winter (<=3 fish/fyke), the highest in summer (up to 58 CPUE) with an intermediate abundance in spring (<=10 CPUE). Follow-up sampling for *Anguilla reinhardtii* and *Parachromis managuensis* failed to capture additional individuals.

DISCUSSION

The current study has revealed that an additional ornamental introduced fish species has become established in Western Australia adding to those known in the region (Beatty & Morgan 2013, Duffy *et al.* 2013, Hourston *et al.* 2014). Although two additional species were detected, they have not become established. The southern platy, *Xiphophorus maculatus*, is a popular aquarium fish that originates from Central America and can survive in a wide range of habitats (Kallman 1975). Although a tropical species, experimental trials have shown it can tolerate waters of approximately 9.5°C to 40°C (Prodocimo & Freire 2001). At the times of sampling, water temperatures were between 18.5°C and 31.1°C, well within the tolerance limits for this species (Prodocimo & Freire 2001). The fluctuations in catches between seasons, indicates abundance may be related to season and/or water temperature and associated reproductive cycles (Milton & Arthington 1983).

X. maculatus was captured in Bodkin Park, Waterford, within an up-steam and downstream lake, as well as the connecting channel, all of which drain directly into the Canning River during flow events, and also in nearby Sandon Park. As an ornamental species, the introduction pathway is likely to be through aquarium release/s. The Canning River is likely to provide a barrier to its spread for much of the year with salinity levels at the confluence well above 3 ppt (Department of Water – Water Science Branch 2013), significantly greater than the species' salinity tolerance (e.g., Englund 2002). However, following heavy rains, salinity at this point can drop below 3 ppt (Department of Water – Water Science Branch 2013), such that *X. maculatus* could spread into the river and other connected waterbodies.

X. maculatus has been assessed as having a very high risk of establishment (Bomford & Glover 2004, Bomford 2008) and where it has established in Queensland, it is assessed as a high risk to native species as it consumes fish fry (Mackenzie *et al.* 2001). It has also established populations in several other countries; however, there is very little information on their impact. Given the potential for the species to spread into the Canning River, and its current restricted distribution, an eradication effort utilising rotenone is urgently required.

A single adult specimen of *A. reinhardtii* was captured in the lake at Lacepede Park, Hillarys. This species occurs naturally on the east coast of Australia from Cape York to Tasmania as well as Lord Howe Island, New Guinea and New Caledonia (Beumer 1996, Allen *et al.* 2003). It is a large species that can reach over 1.6 m and weigh up to 22 kg (Beumer 1996). The species is catadromous and migrates from freshwaters to the sea to spawn with the larvae and then juveniles making their way back to the coast and upstream into freshwater (Merrick & Schmida 1984). Therefore it is unlikely that this species would have been able to establish a population in Western Australia, even if more than one specimen was present.

Compared to the more popular *Anguilla australis*, the international and domestic market for *A. reinhardtii* as a food item is small (Harrington & Beumer 1980) and it is not thought to be in the aquarium trade in Western Australia. Therefore, there appears to be two possible explanations for the presence of this eel in Western Australia: natural range expansion or illegal release from the restaurant trade. A natural range expansion seems unlikely; however, it has shown previous large increases in range with new detections in New Zealand (a 400 km eastward range expansion, Jellyman *et al.* 1996). Similar occurrences are known in both the Galapagos (McCosker *et al.* 1997) and Hawaii (James & Suzumoto 2006). The species had not previously been recorded from either island and whilst the Galapagos occurrence was deemed a natural range expansion (McCosker *et al.* 1997), its presence in Hawaii was concluded to be a result of a natural migration (James & Suzumoto 2006). Given the distance from the source population, and the lake in which the animal was caught in Western Australia has no connection to the ocean, it is unlikely that the presence of this species is due to migration but is almost certainly the result of the release of a captive specimen probably imported for the restaurant trade.

The tropical cichlid, *P. managuensis*, a piscivorous species originally from Central America (Bussing 1998), was found in the lake at Hyde Park, North Perth. This is the first record of this species in the wild in Australia. One characteristic that is unfavourable for the establishment of this species in the Perth region is its tolerance to waters between 25°C and 36°C in its native habitat (Bussing 1998). Winter temperatures of waterbodies in Perth during this survey were as low as 11.7°C and at the time of capture was 27.5°C, so it is possible that the fish was a recent release that had not been present in the wild over winter. However, assessment of temperature tolerances should be used with caution when based on natural ranges as the actual tolerance of a species may be much lower than that reported from its native range and it may simply not have been tested. For instance, the tropical cichlid *Geophagus brasiliensis* has become established in Perth waterways, despite the Mediterranean climate (Beatty *et al.* 2013).

As only a single specimen of *P. managuensis* was caught by the initial sampling, and follow up sampling failed to detect further specimens, the initial detection may also represent its eradication. Nevertheless, if a population of this species were to establish within Western Australia it would present a serious threat. It grows to more than 45 cm (Bussing 1998), much larger than most of the native species in the south-west of Western Australia (Morgan *et al.* 2014), is highly predatory (Dunseth & Bayne 1978, Acosta-Nassar & Günther-Nonell 1992) and can survive in environments with low oxygen (Acosta-Nassar & Günther-Nonell 1992) including stagnant pools (Bussing 1998). The species aggressively defends breeding territories (Günther-Nonell & Boza-Abarca 1994), is highly fecund with a single female able to produce up to 6000 eggs in a single spawning event (Günther-Nonell & Boza-Abarca 1994) and can spawn multiple times throughout a year, as frequently as every 25 days (Günther-Nonell & Boza-Abarca 1994).

The current study has again highlighted that the deliberate release of aquarium fish into waterways poses a significant threat to the Western Australian environment (Morgan *et al.* 2004, de Graaf & Coutts 2010, Beatty & Morgan 2013, Beatty *et al.* 2013, Duffy *et al.* 2013, Hourston *et al.* 2014, Morgan *et al.* 2014). Early detection is the key to eradication—without early detection, there is little chance of a successful eradication as experienced with *Geophagus brasiliensis* in Perth. This species was first reported in 2006 (de Graaf & Coutts 2010, Beatty *et al.* 2013) but early containment and control attempts have been unsuccessful, despite continuing efforts. In 2009, specimens were reported from the Swan River, and by 2013 the species had spread over approximately 20 km. By that stage any control within this system was impossible so efforts then focussed on closing connections to other catchments to prevent it spreading further.

Whilst early detection is essential for eradication, it is problematic due to the cost of physically sampling fish assemblages in the large number of waterbodies present in the both the metropolitan region and the State, including the need for constant and repeated efforts. To reduce costs associated with physical sampling, current attempts are focused on developing cheaper indirect methods of detecting species presence through the use of environmental DNA (Thomsen *et al.* 2012). Although a potential improvement, one disadvantage of this approach is that it is still reactive and does not prevent the initial release, establishment or spread of introduced species.

Community education is an important tool to prevent new freshwater fish introductions globally (Strayer 2010). Approved fish species allowed for import into Western Australia are on the Australian Government, Department of Environment "Live Import List". There are, however, many species already in circulation in the aquarium industry within the State that are not on this list. In an attempt to mitigate the potential impacts of these species, the Western Australian Department of Primary Industries and Regional Development has utilised an education campaign, i.e. the "Don't dump that fish" program. This campaign aims to raise awareness of the potential impact of released aquarium fish and provide education about the options for the disposal of unwanted specimens. Whilst education is a useful tool, the problem remains that a single release can lead to establishment and spread of introduced species, therefore additional options need to be considered.

The continued construction of wetlands in urban areas provides more habitats for the release of unwanted fish, putting native species at risk if introduced species spread. If lakes are to continue to be included in urban developments, several aspects need to be addressed to reduce the opportunity for establishment and spread of introduced fish species in these systems. Options include stocking permanent lakes with native species to provide better control of mosquitos (Lawrence *et al.* 2016) and aquatic life for people to observe. Lakes should be designed to minimise chance of survival or reproduction of non-native species through manipulation of depth, structure, shading and temperature; regular surveys should be undertaken and species eradicated/restocked if required; and ongoing education campaigns using community media and signage should be implemented to highlight the damage caused by releasing introduced species. In addition, alternate designs for storm water management should be considered such as underground stormwater capture and storage; introduced fish cannot establish populations if there are no options for release.

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Influence of fire-age mosaics on macrolichens and bryophytes in southwestern Australia

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ABSTRACT

Lichens and bryophytes are important groups of organisms in almost all natural ecosystems in that they contribute to carbon and nitrogen cycles, and the formation, stability and infiltration properties of soils. Few Australian studies include the response of these organisms to fire at landscape scales. Here we report on the response of cryptogams to post-fire age and its heterogeneity (i.e., a mosaic of fire ages compared to a single fire age) across jarrah forest blocks in southwestern Australia. Three vegetation units were sampled within each of two adjoining forest blocks of 5000 and 6700 ha. Samples were collected in 2005 and 2010, 2.5 and 7.5 years after wildfire in the northern forest block. The other forest block was burned to produce mosaics of fire ages that differed in structure between sampling in 2005 and 2010. The northern block was sampled in two sub-blocks, each with two replicate sample grids of the three vegetation units (12 sample grids), whereas the mosaics were similarly sampled (six sample grids) in the southern block. Each sample grid consisted of four 2 × 50 m plots within which the presence–absence of species within the total area sampled (400 m^2) was recorded. Sixty-seven species were recorded from 36 samples: 40 macrolichens, 20 mosses and seven liverworts. We examined effects of vegetation unit, fire age and heterogeneity on the composition of cryptogam assemblages using Per MANOVA. Cryptogam assemblage composition and richness were associated with vegetation units within jarrah forests and they varied with time since fire. Lichen and bryophyte richness was greatest in landscapes composed of a mosaic of post-fire seral stages and least in pyrically homogenous landscapes 2.5 years after fire. The influence of fire age on cryptogam species richness and assemblage compositions in the deliberately created mosaics is a practical demonstration of the ability of such a landscape to conserve long unburned patches and provide a range of seral stages to maintain cryptogam diversity.

KEYWORDS: assemblage composition, cryptogam, fire heterogeneity, landscape, lichens, liverworts, mosses, patch, refuges, seral stages

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INTRODUCTION

Bryophytes (mosses and liverworts) and lichens, collectively referred to as cryptogams, are susceptible to fire because their preferred habitat is potentially vulnerable to the flame zone and are known to be fire sensitive (Kantvilas *et al.* 2015). However, they persist in Australian ecosystems subjected to periodic fire events. Southwestern Australia contains large areas of flammable native vegetation which, combined with its Mediterranean-type climate of hot dry summers, makes it one of the most fire-prone regions in the world (Burrows & McCaw 2013). The region is also recognised as a biodiversity hotspot (Hopper & Gioia 2004, Rix *et al.* 2015) where fire plays a key role as a selection process (Burrows & Wardell-Johnson 2003, Hopper 2003, He *et al.* 2011), in redistributing nutrient resources (Hingston *et al.* 1989), and competition between plant species (Pekin *et al.* 2012a, b). The coarse filter of periodic fires in these ecosystems from pre-human to more recent times is likely to have pre-conditioned the biota to persist despite recurrent fire intervals varying from short (less than 5 years) to long (at least 30 years). This conditioning has probably contributed to the observed resilience of the south-west ecosystems to fire (Burrows & Wardell-Johnson 2003, Wittkuhn *et al.* 2011).

Pre-European fire regimes practised by indigenous Australians were characterised by frequent low-intensity fires in the drier parts of the jarrah forest and forest margins (Hallam 1975, Burrows *et al.* 1995, Abbott 2003). Regular and frequent introduction of low-intensity burning, where there are patches of regenerating vegetation that will not carry fire, is likely to have developed a mosaic of vegetation at different seral stages from recently burnt patches to long unburnt patches. These mosaics may have limited the spread and intensity of fires under severe burning conditions.

Since the 1960s prescribed fires have been used extensively as a management practice to reduce fuel load to protect State forest, reserves, and adjoining private property from high intensity fires and more recently to maintain species diversity (Burrows & McCaw 2013). The premise that mosaics of varying fire ages might lessen fire spread prompted the Department of Biodiversity, Conservation and Attractions to investigate if employing frequent applications of fire across an entire forest block would emulate the outcomes of the Aboriginal style of burning, including if this would help limit the spread of intense bushfires (cf. Boer *et al.* 2009). The deliberate fire management strategy of patch mosaic burning is postulated to promote biodiversity by providing a range of habitats with different fire histories, qualities, and seral stages at a given scale (Parr & Andersen 2006, Burrows 2008, Stein *et al.* 2014). Such mosaics provide refuges during and after fires, retain propagule sources, and provide stepping-stones for recolonization after fire (Robinson *et al.* 2013). The study was designed with an integrated, multi-disciplinary approach, and included a secondary objective to determine if the mosaic pattern of fire maximized species diversity of vertebrates, invertebrates, fungi, plants and cryptogams at the scale of a whole forest block.

Lichens and bryophytes have a wide range of vital ecosystem functions. These functions include soil formation, soil stabilisation and reducing soil erosion (Cornelissen *et al.* 2007), filtering water (Rieley *et al.* 1979), mobilising minerals and nutrients (Van Heerwaarden *et al.* 2003), extracting and fixing nitrogen from the atmosphere (Kershaw 1985), and providing cover and forage for invertebrates and other small animals (Asplund & Wardle 2016, Glime 2017). In sclerophyll forests, their habitat includes soil, rock, bark, leaves, logs and tree trunks and, where there is a relatively cool microclimate with adequate humidity, leaves and branches of understorey shrubs.

Processes that influence how an ecosystem responds to disturbance include the fundamental processes of species dispersal, colonization, and establishment (Mittelbach & Schemske 2015). A fire has the potential to remove or modify the condition of the habitat and to impact cryptogams through direct exposure of the organisms to flame and heat. Following fire, recolonization of cryptogams relies on the fallout of airborne propagules from unburnt source areas (e.g., for lichens Nascimbene *et al.* 2017, and for bryophytes Hutsemekers *et al.* 2008, Baker *et al.* 2013, Barbé 2016), and 'chance' for suitable conditions in the burnt area (e.g., for lichens Werth *et al.* 2006, and for bryophytes Smith & Stark 2014).

The severity of impact and recovery time is linked to fire intensity and scale (Pharo *et al.* 2013). Low-intensity fires leave unburnt patches with cryptogams (Hylander & Johnson 2010 for bryophytes; Ray *et al.* 2015 for lichens) and provide both unaffected and new habitats for species that prefer early to late successional periods. By comparison, intense fires denude the landscape of cryptogam species (Pharo *et al.* 2013 for bryophytes; Ray *et al.* 2015 for substrate specialized lichens). For many species, suitable conditions enabling recolonization are likely only after the vascular flora has at least partially recovered to particular seral stages (Turner *et al.* 2011 for bryophytes; Kantvilas & Jarman 2012 for bryophytes and lichens).

This study investigates the response of cryptogams to fire, particularly species richness and assemblages in a landscape comprising a diversity of post-fire seral stages including long unburnt refuges compared to one of a uniform seral stage recovering from an intense fire. We assessed variation in species richness and assemblages with time since the last fire, and across land systems that are surrogates for broad vegetation units (Mattiske & Havel 1998, 2000). Four hypotheses were tested within measurement grids for each of mosses, liverworts and macrolichens: (i) species assemblages (i.e., richness and composition) are not affected by vegetation type; (ii) species assemblages are not affected by fire age or (iii) heterogeneity in fire age; and (iv) species assemblages do not predict fire age or heterogeneity in fire age.

METHODS

Study area

The study was conducted across London (34°48'S, 116°55'E) and Surprise forest blocks 30 km northeast of Walpole, covering ~5000 and ~6700 ha respectively,

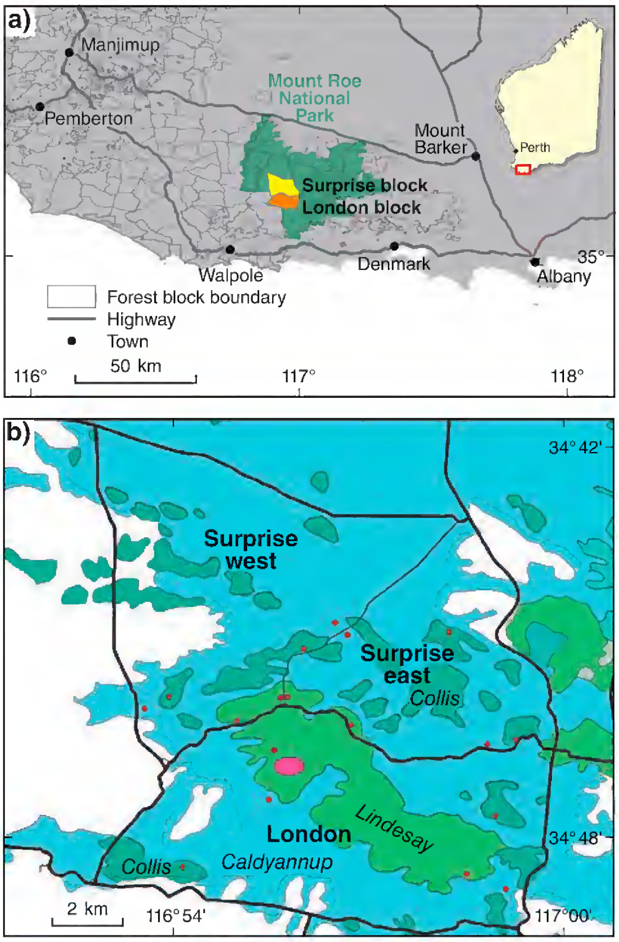

Figure 1. a) Location of the study area at London and Surprise forest blocks, south-west Western Australia; b) Location of sample grids (●) within London and Surprise forest blocks, and vegetation units. Bold lines are forest block boundaries along tracks; Sampled vegetation units of Mattiske and Havel (1998) in London and Surprise blocks denoted thus: Collis (🟩); Lindesay (🟩), (🟥); and Caldyannup (🟦). White areas are un-sampled minor vegetation units in London and Surprise.

within Mount Roe National Park in the south-west of Western Australia (Figure 1a). The region experiences a Mediterranean-type climate with cool wet winters and warm dry summers (Gentilli 1989). Mean annual rainfall is ~1100 mm, most of which falls over the winter months. Mean monthly temperatures range from 15°C to 26.7°C (Bureau of Meteorology 2016).

The soils and landforms of the study area are derived from granitic gneiss (Churchward *et al.* 1988). Landforms are sharply delineated and form a catena of well-drained ridge and hillslope units, respectively named Collis and Lindesay, and poorly drained swampy slopes, plains and drainage floors named Caldyannup (Churchward *et al.* 1988; Figure 1b). Vegetation on the Collis and Lindesay landform units is mostly open eucalypt forests to 30 m dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) with a dense, shrubby understory to two metres tall. The presence of stumps and stump coppice indicated some areas of Collis and Lindesay vegetation were subject to a light and selective jarrah harvest probably during the 1960s (Heberle 1997). Vegetation associated with the Caldyannup landform consists mostly of a variety of reed-dominated seasonal wetlands and heathlands of myrtaceous shrubs to 2 m (Mattiske & Havel 2000).

Fire treatments

The Surprise and London forests blocks are similar, forming a continuum of land systems and vegetation associations, but differed in the fire regimes imposed on them. Prior to the study London block was burnt by low-intensity spring fires in 1994 and 2002. Before 1994, fires within this block were six to nine years apart in spring (Wittkuhn & Hamilton 2010). Further prescribed burns introduced into London block in 2002, 2004, 2006 and 2008 were an attempt to create a fine-scale mosaic of different seral stages since the last fire (Table 1, Figure 2). By 2010, there were patches of vegetation from a few to several hundred hectares ranging from relatively recently burnt to long unburnt (Burrows & Middleton 2016). Thus, sampling London block in spring 2005 and spring 2010 incorporated different fire-age mosaic configurations.

Fire intensity across London block varied from low, with scorch height less than six metres, to high with full canopy scorch. Intensity was further indicated by the removal of different layers of fuel (Gould *et al.* 2007). Landsat imagery with a pixel resolution of 30 m before and after burn applications was used to map the extent and location of different categories of fire treatment (Figure 2). The extent of burnt patches and loss of vegetation cover were determined from Normalised Difference Vegetation Index (NDVI; Li *et al.* 2001). Field data (e.g., canopy scorch, tree mortality, defoliation heights, fuels consumption, ash cover) helped test these indices across a variety of vegetation to check their accuracy.

Surprise block, which adjoins London block, was burnt by a single fire event by an intense bushfire in March 2003 (Wittkuhn & Hamilton 2010) and had no further fire until spring 2011 when a prescribed burn covered its eastern portion. The 2003 fire was intense enough to cause spalling of exposed granite and complete combustion of crown foliage. Previous fires on Surprise were mostly in spring at intervals of six to nine years. Prior to the March 2003 fire two areas within Surprise, affecting only one Lindesay grid, had fires less than five years apart (Wittkuhn & Hamilton 2010). Thus, sampling Surprise block in spring 2005 and spring 2010 covered two homogenous areas with fire ages of 2.5 and 7.5 years, respectively.

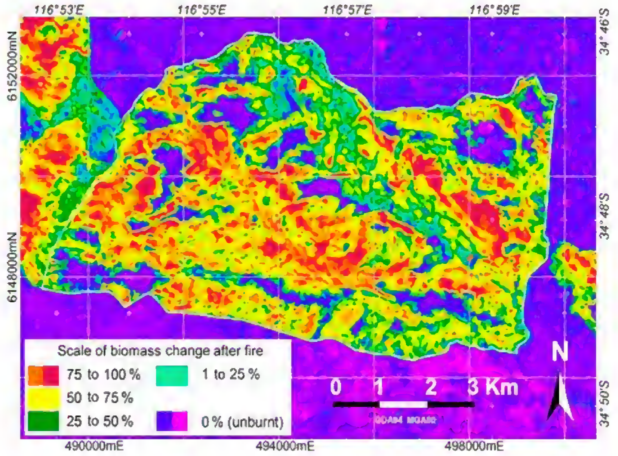

Figure 2. Mapping of burn severity using NDVI classifications in London forest from 2003 satellite imagery following a prescribed fire in spring 2002 (Source: Department of Conservation and Land Management). Note: two unburnt vegetation categories have different reflectances.

Sample grids

A network of sample grids was established as part of a broader fire ecology study (Burrows & Wardell-Johnson 2004, Burrows & Middleton 2016). The network consisted of 18 two hectare (200 m x 100 m) biodiversity sample grids (McCaw *et al.* 2011) established in the three major land systems described above in both London (six grids: 3 vegetation units × 2 replicate grids) and Surprise blocks (Figure 1b). Surprise block had east and west sub-blocks to accommodate planned fire regimes imposed later than the present study (2 × 6 grids: two sub-blocks × three vegetation units × two replicate grids). The initial placement of grids targeted each of the three main vegetation units (Collis, Lindesay, and Caldyannup) within areas of at least 10 ha, and maximum fire age contrasts within London forest block. Although the vegetation units are not of equal extent in the two forest blocks (Figure 1b), each vegetation unit was equally represented in samples from London forest block and Surprise east and west sub-blocks (Table 2).

Species list

An initial survey of lichen and bryophytes was conducted in 2005 to compile a list of species, collect vouchers, and to provide experience for field and lab identification for mosses, liverworts, and macrolichens. This involved collecting specimens along the perimeter of each of the two-hectare grids. The area within the grids was not searched to preserve the integrity of the cryptogam flora for periodic sampling following fire treatments.

Cryptogam response

In 2005, four larger plots (2 × 50 m and a minimum of 50 m apart) were established around the perimeter of the one hectare central part of the sample grids. These two-metre-wide transects were used because they were easily scanned by a single surveyor (R J Cranfield) and their start and finish were defined by permanent pegs established as part of the broader biodiversity survey. Previous sampling in jarrah forest (Cranfield *et al.* 2011) and sampling in the initial survey described above indicated these four 100 m^2 plots would provide sufficient sampling intensity at the local scale. The presence or absence of each species was noted within the combined area of the four plots. The same experienced surveyor who assessed the grids in 2005 reassessed them in 2010. Time taken to survey plots was flexible and depended on richness and abundance of species. Time available to sample individual plots was not limited. Bryophytes and lichens were sampled at the same time. New or unknown species were collected for further investigation and identification in the laboratory. A conservative approach to field identification was taken with the collection of vouchers and later identification in the laboratory against voucher specimens, catalogued specimens in the Western Australian Herbarium (PERTH), and taxonomic literature. Laboratory identifications of species were by R J Cranfield in consultation with C Cargill and J Elix for some specimens of lichens and liverworts. The primary taxonomic literature used for species identifications included: Catcheside (1980), Buck *et al.* (2002), McCarthy (2006) for mosses; Scott (1985), Glenny & Malcolm (2005) for liverworts; George (1992), Grgurinovic (1994), Lumbsch *et al.* (2001), McCarthy (2001), McCarthy & Malcolm (2004), McCarthy & Mallett (2004), McCarthy (2009) for macrolichens. Vouchers of all collected species are lodged in the Western Australian Herbarium, (PERTH).

Frequency of substrates

Twenty plots of one square metre were established at 10 m intervals along two sides of the central hectare of each grid and the presence or absence of habitat substrates on each plot noted in 2010. The substrates investigated were wood, bark, termite mound, soil, rock, organic matter (other than wood or bark), and charcoal.

Analysis

Before analysis, the data were arranged into a repeated measures design of two forest blocks sampled in spring 2005 and 2010. Fire heterogeneity was confounded with forest block, and fire age was confounded with the year of a sample in Surprise block yielding four unreplicated fire-age heterogeneity categories (Tables 1 & 2). Data used was species presence–absence on grids in the combined four 100 m^2 plots. Data were analysed using the permutational multivariate analysis of variance (PerMANOVA) with forest block (confounded with fire age and heterogeneity), vegetation unit, sample grid nested in block by vegetation unit, and year of sample (confounded with time since fire in Surprise block), as main effects (Anderson *et al.* 2008, Clarke & Gorley 2006). PerMANOVA is analogous to a conventional multivariate analysis of variance (MANOVA), where presence or absence of a species is treated as an individual attribute of a sample grid, but significance values in PerMANOVA are determined by randomisation resulting in Pseudo-*F* and P_{Perm} estimates. In contrast to conventional MANOVA, the only underlying assumption is that sample grids are interchangeable (i.e., they have the same species composition) if the null hypothesis is true (Anderson *et al.* 2008). For all PerMANOVA analyses, Type III sums of squares were used with unrestricted permutation of the raw data for 9999 permutations. Specifically, we tested the hypotheses that time since last fire (determined by the year of sampling for Surprise block), fire heterogeneity (forest block), and vegetation unit had no effect on the species assemblage. We analysed mosses, liverworts and lichens separately. Where significant main effects were detected, we conducted pairwise tests using PerMANOVA to identify which vegetation units, fire heterogeneity, or fire ages were significantly different.

Because the effects of fire heterogeneity and forest block were confounded we attempted to isolate forest block effects due to habitat substrates (both utilized and unutilized) using data from London and Surprise blocks collected in 2010. By 2010, 7.5 years after fire in Surprise, fire effects on substrate availability were assumed to be minimal, thus revealing forest block effects on substrate availability. Counts of substrate frequencies were normalized and a PerMANOVA was conducted on the Euclidean distance between grids for substrate composition to determine the effects vegetation unit and forest block (Anderson & Robinson 2003).

Where vegetation unit had a significant effect on the composition of assemblages we calculated the frequency of grids where each species was found in the combined forest (Collis and Lindesay) and Caldyannup vegetation

Table 1. Years when cryptogams sampled in relation to preceding fire regimes on London and Surprise forest blocks.

Forest block	Older pre-sample fires	Younger pre-sample fires	Sample 2005	Additional fires	Sample 2010
London	Spring fires at intervals of 6 to 9 years leaving unburnt patches	Spring 1994, Spring 2002, Autumn 2004, all leaving unburnt patches	Samples from a mosaic of fire ages	Autumn 2006, Summer 2008, both leaving unburnt patches	2005 grids resampled. Samples from a mosaic of fire ages
Surprise	Spring fires at intervals of 6 to 9 years leaving unburnt patches	Intense wildfire March (Autumn) 2003 leaving few if any unburnt patches	All samples taken from areas intensely burnt in March 2003	No further fires	2005 grids resampled. All samples taken from areas intensely burnt in March 2003

Table 2. Time since fire in the sampled grids and forest blocks. The design can be considered as a repeated measures design (the same grids sampled in 2005 and 2010), with fire-age heterogeneity confounded with forest block (London presented heterogeneity within and between measurement grids in fire age, and Surprise homogeneity of extensive and intensive wildfire).

Forest block	**Vegetation unit**	**Fire ages within sample grids in sample year 2005**		**Fire ages within sample grids in sample year 2010**	
		Replicate grid A	**Replicate grid B**	**Replicate grid A**	**Replicate grid B**
London	Collis	≥20	≥20, 3	≥25, 4.5	≥25, 8, 4.5
	Lindesay	≥20	3	≥25, 4.5, 2	4.5
	Caldyannup	3	3	8, 2	8, 2
Surprise east	Collis	2.5	2.5	7.5	7.5
	Lindesay	2.5	2.5	7.5	7.5
	Caldyannup	2.5	2.5	7.5	7.5
Surprise west	Collis	2.5	2.5	7.5	7.5
	Lindesay	2.5	2.5	7.5	7.5
	Caldyannup	2.5	2.5	7.5	7.5

units. The small size of the data set allowed Fisher's exact tests (1-tail) to be conducted on the raw presence–absence data to determine the independence of this categorization from vegetation unit. Indicator values were calculated (as per Turner *et al.* 2011 to overcome differences in sample sizes) for the vegetation categories of each species where significant dependence was detected.

We categorized the combined forest (Collis and Lindesay) vegetation units by the fire-age heterogeneity categories defined by forest block and year of sampling and determined indicator values. We selected grids on London where some area of age ≥ 20 years was present (6 sample grids: Table 2) and pooled the two years of data (2005 and 2010) from London into one fire-age category defined by having at least some area of age ≥ 20 years. Sparse replication rendered a similar analysis for Caldyannup vegetation unit as impractical.

RESULTS

Species richness

Sixty-seven species of cryptogams were recorded from all sampling grids within London and Surprise blocks comprising 40 lichen, 20 moss, and seven liverwort species. More species of lichen were detected in Lindesay and Caldyannup vegetation units in 2010 than in 2005 (Table 3, Appendix).

We compared species richness of Surprise block (single fire age) with that of London block (mosaic of fire ages). Surprise east and west forest sub-blocks each contained a total of 10 species of lichen and bryophytes 2.5 years after the intense bushfire, which was about one-third of that found for the same sampling effort for the London mosaic containing fire ages of 3 and ≥20 years (Figure 3a). Fewer species were found on Surprise east and west in 2010, 7.5 years after the fire, than on London block sampled in 2010 with comparable sampling efforts (Figure 3a). At the sample grid scale, species richness increased in Surprise block between 2005 and 2010, whereas species richness per grid in London remained stable during that period (Figure 3b). Paired *t*-tests (1 tail) revealed significant differences between 2005 and 2010 in number of species per grid on Surprise east ($t_{(5)}$ = -14.16, $P \geq 0.001$) and Surprise west ($t_{(5)}$ = -4.49, $P = 0.003$), but not London ($t_{(5)}$ = -1.25, $P = 0.13$). Within 7.5 years after fire in Surprise, average richness on grids was similar between London and Surprise blocks (Figure 3b).

Table 3. The number of lichen, moss and liverwort species for the three vegetation units Collis, Lindesay and Caldyannup from the 2005 and 2010 assessments.

	2005			**2010**			
	Collis	Lindesay	Caldyannup	Collis	Lindesay	Caldyannup	Total
Number of grids sampled	6	6	6	6	6	6	2 × 18
Lichen	17	8	8	18	17	16	40
Moss	10	9	6	11	11	7	20
Liverwort	5	3	4	4	4	4	7
Total	32	20	18	33	32	27	67

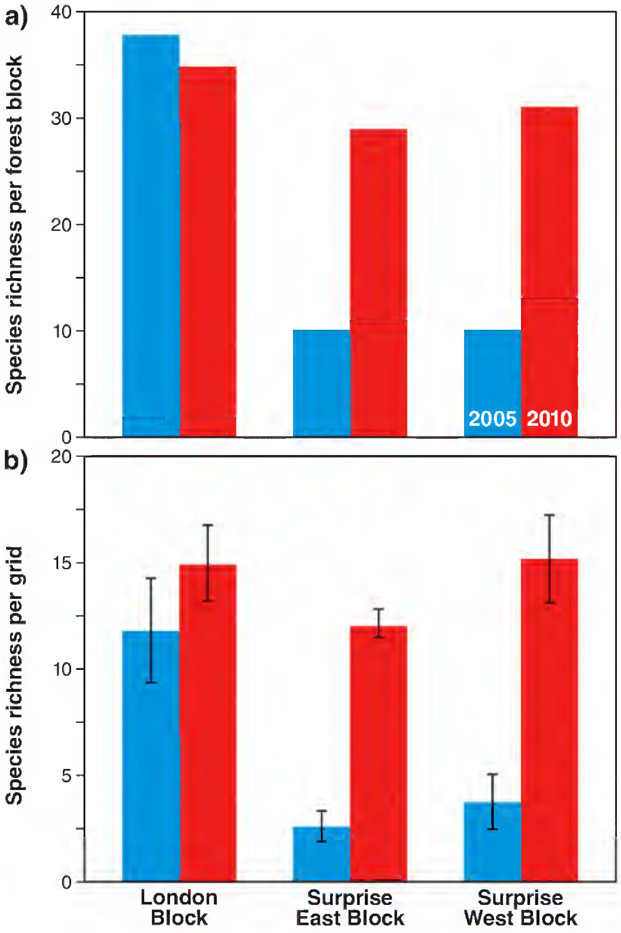

Figure 3. Comparisons of cryptogam species in London, Surprise east and Surprise west forest blocks for 2005 and 2010 measurements. Sampling intensity for each category in both sets of measurements were equivalent: **a**) Total number of cryptogam species (note that fire ages in London are mixed for both years); **b**) Average number of cryptogam species per sample grid. In London mosaics fire ages range from 3 to ≥ 20 in 2005 and 2 to ≥ 25 years in 2010. In Surprise, fire ages were 2.5 years in 2005 and 7.5 years in 2010. Thin bars indicate ± standard error of the mean.

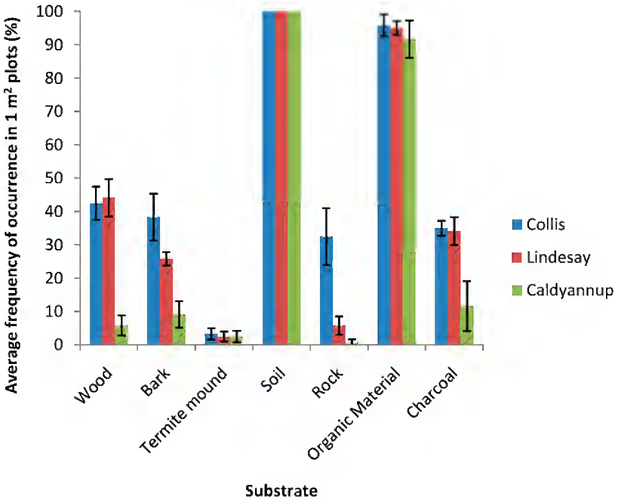

Figure 4. Habitat composition by vegetation unit for London and Surprise forest blocks in 2010. Thin bars indicate ± standard error of the mean.

Substrate availability

By 2010 there was no significant difference between London and Surprise blocks in the composition of available habitat types. There were differences in habitat composition according to vegetation unit (Pseudo-F = 5.65, P_{Perm} = 0.0001) and each vegetation unit showed a unique composition of habitat types. Pairwise comparisons were as follows: Collis and Lindesay, t = 1.618, P_{Perm} = 0.03; Collis and Caldyannup, t = 2.858, P_{Perm} = 0.0002; Lindesay and Caldyannup, t = 2.44, P_{Perm} = 0.0003. Exposed rock is virtually absent within the Caldyannup units, whereas both bark cover and rock are more prevalent in Collis units than Caldyannup and Lindesay units. Wood, bark and charcoal were least abundant in Caldyannup units (Figure 4).

Vegetation and fire influences

Vegetation unit had a significant effect on assemblages of mosses, liverworts, and macrolichens (Table 4). Differences between assemblages among vegetation types are summarised in Table 5. Collis and Lindesay vegetation units were indistinguishable from each other in species assemblage. Both Collis and Lindesay had different species assemblages of mosses, liverworts, and macrolichens to Caldyannup units (Table 5). Forest block (confounded with fire heterogeneity) had a significant effect on moss and macrolichen but not liverwort assemblages (Table 4). Year of sampling (delimiting fire age in Surprise block) had a significant effect on assemblages of all three life forms. Block by year interaction had a significant effect on assemblages of all three life forms. Differences in assemblages among forest block and year of sampling combinations which define the four fire treatments are summarised in Table 5. On Surprise block fire ages of 2.5 and 7.5 years consistently differed in species assemblages for all three life forms. On London block mosaic fire treatment categories London mosaic 2005 and London mosaic 2010 were indistinguishable in species assemblage for liverworts, but not mosses and lichens. Comparing London and Surprise blocks within sample years, fire treatment categories Surprise age 2.5 and London Mosaic 2005 were different in assemblages of mosses and lichens and indistinguishable for liverworts. Fire treatment categories Surprise age 7.5 and London mosaic 2010 were indistinguishable in species assemblage for mosses and lichens and different for liverworts.

Species assemblage predicts vegetation unit and fire age?

The frequencies of some species is dependent on the vegetation unit (Tables 6), fire age, or fire-age heterogeneity (Table 7). There were three species with a preference for Caldyannup and two species which preferred forest vegetation units (Table 6). Five species were early colonizers after the wildfire in the forest vegetation units (Table 7). Of these, the liverwort *Cephaloziella exiliflora* and the moss *Campylopus introflexus* had their greatest abundance on older seral stages. Seven

Table 4. Effects of forest block (London and Surprise, which is confounded with fire heterogeneity treatments), vegetation unit (Collis, Lindesay, and Caldyannup), sample grid (nested within forest block and vegetation unit), and year of measurement (2005 and 2010) on moss, liverwort, and macrolichen assemblages based on Bray-Curtis similarity matrices analysed by PerMANOVA. Degrees of freedom (df) define the effective rather than nominal sample sizes for effects and their interactions.

Effect	df	Mosses	Liverworts	Macrolichens
		Pseudo-*F*, P_{PERM}	Pseudo-*F*, P_{PERM}	Pseudo-*F*, P_{PERM}
Block	1	2.862, 0.03	3.611, 0.06	4.893, 0.005
Vegetation unit	2	3.528, 0.003	5.111, 0.009	2.684, 0.02
Block x Veg	1	2.023, 0.06	1.882, 0.17	1.752, 0.10
Grid(Block x Veg)	13	1.222, 0.26	2.232, 0.03	0.828, 0.72
Year	1	5.002, 0.003	9.506, 0.0009	21.459, 0.0001
Block x Year	1	5.172, 0.002	4.528, 0.02	5.342, 0.008
Veg x Year	2	0.522, 0.82	4.849, 0.006	1.502, 0.19
Block x Veg x Year	2	1.896, 0.09	Excluded	1.115, 0.35
Residual	11, 13, 11	_	_	_

Table 5. Pairwise comparisons of assemblages based on a Bray-Curtis similarity matrices analysed by pairwise PerMANOVA with forest block (London and Surprise, which is confounded with fire heterogeneity treatments), vegetation unit (Collis, Lindesay, and Caldyannup), sample grid (nested within forest block and vegetation unit), and year of measurement (2005 and 2010) as effects.

Assemblages compared	Mosses	Liverworts	Macrolichens
	t, P_{PERM}	*t*, P_{PERM}	*t*, P_{PERM}
Collis, Lindesay	1.329, 0.15	0.653, 0.65	1.208, 0.22
Collis, Caldyannup	2.332, 0.004	3.033, 0.005	2.029, 0.01
Lindesay, Caldyannup	2.141, 0.003	2.262, 0.03	1.496, 0.03
London 2005 (Multiple age mosaic), London Mosaic 2010 (Multiple age mosaic)	1.766, 0.04	1.795, 0.14	1.676, 0.02
London Mosaic 2005 (Multiple age mosaic), Surprise 2005 (Age 2.5)	2.369, 0.004	1.633, 0.09	3.104, 0.002
London Mosaic 2010 (Multiple age mosaic), Surprise 2010 (Age 7.5)	0.381, 0.92	2.566, 0.009	0.757, 0.77
Surprise 2005 (Age 2.5), Surprise 2010 (Age 7.5)	2.990, 0.0004	3.127, 0.002	6.478, 0.0001

Table 6. Indicator species for Caldyannup and forest (Collis and Lindesay) vegetation units. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Species	Life form	Frequency of grids with occurrence (%)		Fishers exact probability of observed or more extreme (1-tail)	Indicator value	
		Caldyannup *N* = 12	Forest *N* = 24		Caldyannup	Forest
Campylopus bicolor	Moss	83	46	0.034	74	41
Geobelobryum unguiculatum	Liverwort	67	17	0.005	73	18
Leptogium sp. (PERTH 06896111)	Macrolichen	50	13	0.022	65	16
Sematophyllum subhumile var. *contiguum*	Moss	0	33	0.024	0	67
Cephaloziella exiliflora	Liverwort	17	67	0.006	18	73

Table 7. Frequency of early colonizers of forest (Collis and Lindesay) vegetation units on Surprise block, and fire-age indicator species within Collis and Lindesay units. London grids include some fire areas ≥ 20 years as well as areas ranging from 2 to 8 years since fire. Early colonizers marked [a], species most strongly indicative of fire age 7.5 years marked [b], and species most strongly indicative of sites containing some fire areas ≥ 20 years marked [c]. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Species	Life form	Frequency of Collis and Lindesay grids with occurrence (%)			Fishers exact probability of observed or more extreme (2 tail, $\alpha = 0.05$)	Indicator value		
		Age 2.5 $N = 8$	Age 7.5 $N = 8$	London grids which include some area of age ≥ 20 $N = 6$		Age 2.5	Age 7.5	London with some area of age ≥ 20
Funaria hygrometrica [a]	Moss	100	100	83	ns	_	_	_
Campylopus bicolor [a]	Moss	25	63	67	ns	_	_	_
Barbula calycina [a]	Moss	25	75	50	ns	_	_	_
Cephaloziella exiliflora [a]	Liverwort	13	100	100	0.0002	9	74	74
Campylopus introflexus [a]	Moss	13	100	100	0.0002	9	74	74
Thysanothecium scutellatum	Macrolichen	0	100	100	0.000006	0	75	75
Cladia aggregata	Macrolichen	0	100	83	0.00002	0	77	64
Cladia schizopora	Macrolichen	0	75	50	0.008	0	68	45
"Grey green slick" PERTH 06320082 [b]	Macrolichen	0	63	17	0.011	0	71	19
Diploschistes scruposus [b]	Macrolichen	0	88	33	0.0008	0	80	30
Hypocenomyce foveata	Macrolichen	0	63	67	0.011	0	55	59
Cladonia rigida [c]	Macrolichen	0	63	100	0.0004	0	50	81

macrolichen species that are relatively common on older seral stages remained absent 2.5 years after fire. The unidentified lichen "Grey green slick" and *Diploschistes scruposus* had high indicator values for a fire age of 7.5 years whereas *Cladonia rigida* had a high indicator value for grids containing some areas with a fire age ≥20 years.

Thirty-three percent of the total cryptogam flora collected was only from London block, which includes areas of mixed fire ages and long unburned substrates. Nine percent of the total flora was found only on Surprise block areas burnt 7.5 years beforehand, and six percent of the total flora was exclusive to Surprise block in areas with a fire age of 2.5 years.

DISCUSSION

Fire age affects species richness and composition

Vascular and woody vegetation composition in the study area is known have a long-term resilience to a variety of fire histories (Wittkuhn *et al.* 2011, Pekin *et al.* 2012b). However, within these habitats severe and extensive wildfires have reduced cryptogram species richness and altered species assemblages of mosses and lichens compared to mosaic fire areas. Changes in species composition and an increase in species richness with time since wildfire are consistent with outcomes reported elsewhere for both eucalypt (Pharo & Beattie 1997, Pharo *et al.* 2013, Kantvilas *et al.* 2015) and other forests (Esposito *et al.* 1999, Ray *et al.* 2015).

Time since fire is likely to contribute to species turnover from early to late-successional species due to changes in habitat suitability and differences among species in habitat requirements (Duncan & Dalton 1982, Esposito *et al.* 1999, Turner *et al.* 2011, Kantvilas & Jarman 2012). This has different consequences where there have been many fire ages rather than a single fire event. The frequent introduction of fire to London forest maintained a range of post-fire succession stages with variations in fire intensity, ages and spatial scales within grids (metres and tens of metres), as well as between grids (hundreds of metres to kilometres). Whereas the composition of liverwort assemblages did not change over time in the mosaics, likely due to the range of refuge habitats maintained (Hylander & Johnson 2010), moss and macrolichen assemblages in the shifting mosaics did change. We have insufficient data to explore the mechanism for this observed difference; however, the development of lichen communities is not neutral with respect to habitat age (Gjerde *et al.* 2012, Nascimbene *et al.* 2017), and the proportions of different fire ages on sample grids within the mosaic varied between 2005 and 2010.

Following the single high-intensity fire event in Surprise block, species showed a successional trend from one seral stage to the next. Early colonists were followed by a period when early and late-successional species tended to coexist. At 7.5 years post-fire in Surprise block, assemblages of mosses and macrolichens but not liverworts were similar to those in London block where there were fire ages ranging from two to ≥ 25 years. Cranfield *et al.* (2011) found sites subjected to controlled fuel reduction fires and timber harvesting in comparable jarrah forest sites had low cryptogam species richness at one to four years after fire. Richness gradually increased until about 10 years after fire. Beyond 10 years after fires, species richness reduced again until species richness was lower than sites only one to four years after fire. They attributed this later reduction of species richness to ground-inhabiting species being covered by leaf litter, and the subsequent loss of substrates suitable for primary colonizers. Both processes affect the availability of suitable habitat with time since fire. The return within 7.5 years of species richness after the severe fire in Surprise block to levels approaching those of the mosaic with ages two to ≥ 25 years might indicate that dispersal or habitat limitation are not operating for most species in the jarrah forest cryptogam flora. We consider the disturbance due to light and selective timber harvesting in the 1960s in the study area was probably small compared to the effects of repeated fire cycles between then and sampling in 2005 and 2010.

London fire mosaic and the 'storage' effect

Responses of cryptogam community composition to fire age in boreal forests in North America are detectable decades and centuries beyond the fire-age range of the present study, whereas species richness in those same communities remained stable in a space-for-time study (Boudrealt *et al.* 2002). Distributions of slowly dispersing cryptogams in contemporary landscapes may reflect historic linkages to source populations of propagules rather than contemporary linkages, thereby concealing an extinction debt (Johansson *et al.* 2013). The imperative to preserve cryptogam species diversity by maintaining a range of fire ages linked to landscape level suggested by Boudrealt *et al.* (2002) is equally applicable to jarrah forest where fire return intervals are shorter. Long fire return intervals in jarrah forest allow build-up of fuels permitting intense and extensive fire events due to the inevitability of ignition and difficulties of fire suppression with heavy fuel loads (McCaw 2013). In that case, the 'storage effect', whereby long unburned patches accumulate the most species or provide unique habitats for some species (Roxburgh *et al.* 2004, Fenton and Bergeron 2008), becomes tenuous.

The consequences of the intense bushfire in Surprise forest was immolation of cryptogam biomass, loss of organic habitat substrates for cryptogams, and loss of habitat from spalling of rock surfaces, all leading to a likely protracted loss of some species from assemblages (Kantvilas & Jarman 2012). The London forest block mosaic exhibited no loss in cryptogam richness per grid over time, was richest when comparing equivalent sampling intensity, and maintained the majority of species exclusive to any fire-age treatment. The conservation of the variety and availability of substrates, including newly available and particularly those long undisturbed by fire such as retained bark and the unburnt surfaces of large coarse woody debris, appeared to be the mechanism for maximizing cryptogam diversity at the forest block scale. We suggest that the fire-age mosaic effect on cryptogam species richness and assemblages within London block is a practical and successful demonstration of how to conserve long unburned patches and maximize cryptogam richness at the forest block scale without elevating the risk of high-intensity fire.

Species assemblage predicts fire age

The presence of some species is dependent on fire-age heterogeneity or vegetation type. Landscape-scale prioritization of cryptogam species conservation based on a mosaic of fire ages within vegetation units has the ability to conserve cryptogam species at risk of reduction at a local and landscape scale. Many species were seldom collected and hence of little predictive value in this study. These species may be of highest concern for fire managers because their scarcity in regional sources of propagules makes them vulnerable to their loss from the landscape where fires are frequent, or severe and extensive (See also Table 3 in Hylander & Johnson 2010). One species, *Cladonia rigida*, was common to grids containing burnt areas ≥ 20 years old, although this species was also present on some grids by 7.5 years after the fire. For many species, recolonization rate compared to fire frequency remains unknown (Wills *et al.* in press), requiring further research at the species and landscape level.

The effects of vegetation type

Cryptogams have the ability to colonize a wide range of substrates. Whereas some are substrate specific, many are able to share a range of substrates (Turner & Pharo 2005, Pharo *et al.* 2013). There is considerable variation in the ability of substrates provided by vascular and woody plants to host cryptogams (Pharo *et al.* 2013). Substrate availability was variable in the London and Surprise blocks as each of the vegetation units had a unique combination of substrates. Caldyannup vegetation unit had the fewest wood, bark, charcoal and rock substrates, which may predispose this unit to be the least rich in cryptogams. Caldyannup grids also differed in moss, liverwort, and lichen assemblages from Lindesay and Collis units. Elsewhere, vegetation type differentiates the community composition of cryptogams (e.g., McMullan-Fisher *et al.* 2010, Ardelean *et al.* 2015). However, other factors potentially correlate with vegetation type (humidity, edaphic characteristics, and substrate availability) and may contribute to substrate use and species assemblages. From our limited data, we were unable to identify any mechanism that allows vegetation type to affect species assemblage and richness.

CONCLUSIONS

In the studied jarrah forest frequent introduction of fire maintained habitats with a mixture of fire ages at both local and landscape scales. This, in turn, maintained cryptogam diversity at those scales. Intense and extensive fire jeopardised some species, resulting in their absence more than 7.5 years post-fire. The recovery of cryptogams is favoured by low-intensity fire as this produces a mosaic of small patches including unburnt areas or in which the heat intensity is low enough to be non-lethal to in-situ propagules.

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APPENDIX

Species of bryophytes and lichens collected from London and Surprise forest blocks in 2005 and 2010 with number of sample grids where they were present. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Taxon	**Life form**	**London 2005 and 2010**	**Surprise 2005**	**Surprise 2010**	**Total number of samples where present**
		Fire age mosaics *N* = 12	**Fire age 2.5 *N* = 12**	**Fire age 7.5 *N* = 12**	***N* = 36**
Funaria hygrometrica	Moss	9	11	12	32
Campylopus introflexus	Moss	10	3	12	25
Campylopus bicolor	Moss	8	4	9	21
Barbula calycina	Moss	4	3	7	14
Othodontium lineare	Moss	3	0	5	8
Sematophyllum subhumile var. *contiguum*	Moss	4	0	4	8
Rosulabryum capillare	Moss	3	0	3	6
Fissidens tenellus var. *tenellus*	Moss	2	0	3	5
Hypnum cupressiforme	Moss	1	0	3	4
Ceratodon purpureus subsp. *convolutus*	Moss	1	1	0	2
Dicranella dietrichiae	Moss	2	0	0	2
Didymodon torquatus	Moss	2	0	0	2
Pleurophascum occidentale	Moss	2	0	0	2
Triquetrella papillata	Moss	0	0	2	2
Dicranoloma billarderi	Moss	0	1	0	1
Rosulabryum campylothecium	Moss	1	0	0	1
Sematophyllum homomallum	Moss	1	0	0	1
Syntrichia antarctica	Moss	1	0	0	1
Thuidopsis sparsa	Moss	0	0	1	1
Zygodon menziesii	Moss	0	1	0	1
Cephaloziella exiliflora	Liverwort	7	1	10	18
Geobelobryum unguiculatum	Liverwort	5	4	3	12
Lethocolea pansa	Liverwort	7	3	1	11
Chiloscyphus semiteres	Liverwort	3	0	3	6
Kurzia compacta	Liverwort	3	2	0	5
Astrella drummonii	Liverwort	0	1	0	1
Riccardia crassa	Liverwort	1	0	0	1
Cladia aggregata	Lichen	9	0	11	20
Thysanothecium scutellatum	Lichen	8	0	12	20
Cladonia rigida	Lichen	7	0	8	15
Cladia schizopora	Lichen	5	0	9	14
Diploschistes scruposus	Lichen	2	0	8	10
Hypocenomyce foveata	Lichen	4	0	6	10
Leptogium sp. (PERTH 06896111)	Lichen	3	0	6	9
Usnea inermis	Lichen	4	0	3	7
"Grey green slick" PERTH 06320082	Lichen	2	0	5	7
Imshaugia aleurites	Lichen	3	0	3	6
Ochrolechia subpallescens	Lichen	4	1	0	5
Cladonia krempelhuberi	Lichen	2	0	3	5
Cladonia sp. London	Lichen	2	0	1	3
Ramboldia stuartii	Lichen	2	0	1	3
Pannoparmelia wilsonii	Lichen	1	1	1	3
Cladonia sulcata	Lichen	1	0	2	3
Buellia dissa	Lichen	2	0	0	2
Hypocenomyce scalaris	Lichen	2	0	0	2
Rhizocarpon sp. grey (PERTH 06324452)	Lichen	2	0	0	2
Notocladonia cochleata	Lichen	1	1	0	2
Glonium circumserpens	Lichen	1	0	1	2

Taxon	**Life form**	**London 2005 and 2010**	**Surprise 2005**	**Surprise 2010**	**Total number of samples where present**
		Fire age mosaics *N* **= 12**	**Fire age 2.5** *N* **= 12**	**Fire age 7.5** *N* **= 12**	*N* **= 36**
Ochrolechia sp. tan doughnuts (PERTH 06319300)	Lichen	1	0	1	2
Ochrolechia subrhodotropa	Lichen	1	0	1	2
Amandinea punctata	Lichen	1	0	0	1
Calicium abietinum	Lichen	1	0	0	1
Cladia inflata	Lichen	1	0	0	1
Cladonia cervicornis var. *verticellata*	Lichen	1	0	0	1
Cladonia ochrochlora	Lichen	1	0	0	1
Cladonia scabriuscula	Lichen	1	0	0	1
Dictyographa sp. brown lips (PERTH 06322301)	Lichen	1	0	0	1
Diploschistes euganeus	Lichen	1	0	0	1
Diploschistes sticticus	Lichen	1	0	0	1
Halegrapha mucronata	Lichen	1	0	0	1
Hypogymnia pulverata	Lichen	1	0	0	1
Pannaria elixii	Lichen	1	0	0	1
Hypogymnia subphysodes var. *subphysodes*	Lichen	0	1	0	1
Ainoa mooreana	Lichen	0	0	1	1
Caloplaca marina	Lichen	0	0	1	1
Cladonia sp. golden coral (PERTH 07320388)	Lichen	0	0	1	1
Tephromela alectoronica	Lichen	0	0	1	1

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Journal of the Royal Society of Western Australia, 100(2): 46–48, 2017

Vale Phillip Elliot Playford

a life of geology, exploration and history

27 December 1931 – 12 July 2017

Phillip (Phil) Elliott Playford was born on 27 December 1931 in Guildford, the elder son of Elliott Geoffrey and Alice Mary Playford. He attended the Forrest Street State School (now South Perth Primary School) (1937–42) and completed his schooling at Perth Modern School (PMS) (1943–48). He later wrote that he 'didn't like the school (PMS)' and that his 'salvation came through tennis, in which I eventually became school champion and captain of the winning team in the inter-school competition'. He won a General Exhibition in the Leaving Certificate exam and went on to study geology at the University of Western Australia (1948–53). His honours project was mapping the Jurassic geology of the Geraldton district. Travelling to and from the field area on his motorbike (a Triumph 3T) he collected a large number of ammonites from the Newmarracarra Limestone which he sent to W J Arkell at Oxford University, who was the world-renowned expert on Jurassic rocks. This led to his first major publication (with Arkell, in the Philosophical Transactions of the Royal Society of London) that established the Bajocian age for this unit.

After graduating, Phil joined the Bureau of Mineral Resources (BMR) in 1953, working in Alan Condon's team with two other stalwarts of WA geology, Murray Johnstone and Daryl Johnstone, mapping the southern Carnarvon Basin. In 1953 WAPET (West Australian Petroleum Pty Ltd) discovered oil at Rough Range, and lured Phil, among others, away from the BMR. In those days oil exploration in Western Australia involved a lot of detailed geological mapping, and Phil has always emphasised the importance of such field work in understanding the geology of a region. This work culminated in McWhae et al's (1958) extended paper which laid the foundations of our modern understanding of the stratigraphy of the major sedimentary basins of the State.

Phil's time with WAPET took him to the Carnarvon and Canning Basins and had four important impacts on his subsequent career. The first was discovering stromatolites at Hamelin Pool in July 1954 when he and Daryl Johnstone were working in the Shark Bay area. This led to his lifelong interest in stromatolites and the geology of the Shark Bay area. The second was meeting stockman Tom Pepper at Tamala station, also in July 1954, who showed him various items that he said came from a shipwreck at the foot of the coastal cliffs south of Tamala. Thus began Phil's involvement with what he eventually deduced was the wreck of the Zuytdorp. Thirdly, in 1956 he was introduced to the Devonian reef complexes, which started a life-long love affair with these superbly exposed rocks. The Aboriginal cave paintings in these Devonian limestones also fascinated Phil, resulting in his research into the mythological significance of the paintings and the mapping of tribal boundaries.

Arising from this interest, in 1964 Phil joined an expedition to the Gibson and Great Sandy Deserts, which successfully located the last known Aborigines who had never before seen Europeans, living almost untouched by the outside world. Phil at times recounted the tale of how, although they had never met Europeans, they knew of "puddy tats", through contacts with other Aborigines.

Phil was awarded a Fulbright Scholarship in 1959 which took him to Stanford University where he obtained a PhD for his thesis on the geology of the Egan Range, near Lund, eastern Nevada. He completed the project in two years and decided to return to Australia. Not long after his return to Perth he met Cynthia Hogbin, with whom he shared a keen interest in the bush; Phil with the rocks, Cynthia with the plants. They married in 1964 and had two daughters, Julia and Katherine.

While WAPET was keen to re-hire Phil, he saw that fieldwork was a lower priority than before, and instead joined the Geological Survey of Western Australia (GSWA, a branch of the Mines Department – now newly renamed the Department of Mines, Industry Regulation and Safety) in 1962, as Supervising Geologist of the newly created Sedimentary (Oil) Division, which had responsibility for mapping the Phanerozoic basins of the State and assessing their fossil fuel resources. He worked for the department in various positions (Assistant Director GSWA 1978–80, Deputy Director GSWA 1980–84, Assistant Director General 1984–86, Director GSWA 1986–92) until his retirement in 1992, except for a short time as Exploration Manager and General Manager of Abrolhos Oil in 1970–71. After retirement, he wrote up his work on the Zuytdorp and continued to work on the geology of the Devonian reef complexes, Shark Bay, and most recently Rottnest Island, from an office in GSWA until late in 2015.

One of Phil's first recommendations in the GSWA was to ask the Minister for Mines to encourage WAPET to drill the anticline below Barrow Island in the Carnarvon Basin. The subsequent discovery of oil in commercial quantities in 1964 marked the dawn of petroleum production in Western Australia. Under his supervision and as part of GSWA Director Joe Lord's drive to map all of WA at 1:250 000, mapping was undertaken in the major Phanerozoic basins, resulting in the publication of several bulletins. Phil continued his work on the Devonian reef complexes of the Canning Basin, soon publishing the first GSWA bulletin on their geology (Bulletin 118) in 1966. He then embarked on detailed studies of significant areas of the reef complexes. One of the early results of this work was the realisation that stromatolites in the marginal slope deposits extended down slope to at least 35 m, and probably more than 100 m water depth; this was in conflict with the prevailing view in the 1960s that stromatolites were intertidal, and renewed his interest in the Hamelin Pool stromatolites where he showed that they also extended into the subtidal region. The Devonian reef complexes were the subject of several lecture tours by Phil, through the USA and Canada in 1978 as an AAPG Distinguished Lecturer; through Australia in 1980 as a PESA Distinguished Lecturer; in China in 1988 as an Exchange Scientist for the Australian Academy of Science and Academia Sinica; and through Europe in 1989 as a Guest Fellow of the Royal Society of London.

An ongoing condition of Phil's acceptance of administrative roles in the Mines Department and its later incarnations was that he be allowed to devote time each year to geological research, primarily field work on the Devonian reef complexes. Regular updates on the geology of the complexes continued through the 1980s and 1990s, together with supervision of PhD and post-graduate projects, until their culmination in 2009 with publication of the second GSWA bulletin on the complexes (Bulletin 145). This also included observations on Permian glacial pavements and subglacial channels, lakes, tunnels, cave systems, tower karst, collapse breccias, and solution dolines. En route to the Kimberley, and as separate short trips, visits to Shark Bay and the Zuytdorp Cliffs continued.

After the second bulletin on the reef complexes, completion of the Shark Bay research became Phil's top priority. The remarkable stromatolites were largely responsible for Shark Bay being declared a World Heritage Area, but were not the only focus of Phil's work. The project grew to include aspects of Quaternary coastal geology around most of WA, but particularly neotectonism and the recognition of the imprint of ancient major tsunamis on WA, from the Kimberley through the Pilbara to Shark Bay, from large cliff-top blocks in coastal areas. Phil concluded that major tsunamis, although infrequent, constitute a significant hazard in coastal areas that has not been adequately included in risk assessments. A comprehensive bulletin, again oriented towards the field geology but also including the history of the Shark Bay region, was published in 2013 (GSWA Bulletin 146). Compilation of a similar bulletin integrating Phil's work on Rottnest Island, was underway in late 2015 when Phil was diagnosed with cancer, and sadly will not be completed. Part of the Rottnest work was updating of a field guide, first prepared in 1988. Phil's final paper, reviewing the history of our understanding of the Canning Basin reef complexes appeared in print in September in SEPM (Society for Sedimentary Geology) Special Publication 107, which is dedicated to his memory.

Phil with colleagues at Windjana Gorge early 1970s

Phil's scientific achievements and work through his career promoting the petroleum prospectivity of Western Australia have been recognized in several awards. These include: Special Commendation Award of the AAPG, Lewis G Weeks Gold Medal of APEA, Gibb Maitland Medal from the Geological Society of Australia, Honorary DSc from UWA, Honorary Membership of RSWA, the Medal of The Royal Society of Western Australia, and Distinguished Honorary Membership of PESA. He was a founding member and Fellow of the Geological Society of Australia, and a Fellow of the Australian Academy of Technology and Engineering. He served geology and other sciences as President of The Royal Society of Western Australia, Australian Petroleum Exploration Association Professional Division (WA), Petroleum Exploration Society of Australia (WA), Australian Geoscience Council, and National Trust (WA). He was also Chairman of the Board, WA Museum of Natural Science, Adjunct Professor of Petroleum Geology, Curtin University, Adjunct Professor of Geology, The University of Notre Dame, and an Honorary Associate of the Geological Survey of WA and the WA Museum.

Although Phil's geological legacy is considerable, he may be remembered by the general public for his contributions to WA's history, principally the early Dutch explorers and aspects of Aboriginal art and heritage. Phil's first tasks after his retirement from Director GSWA were a new phase of fieldwork in the Kimberley, and to complete his work on the Dutch wreck the Zuytdorp (in 1994 Phil and Tom Pepper were officially rewarded by the State as being the co-discoverers of this historic wreck). His 1996 volume "Carpet of Silver" published by UWA Press, received the Premier's Book Award for Historical and Critical Studies in 1997, and was reprinted in 1998 and 2006. He followed this in 1998 with a book on Willem de Vlamingh's voyages, "Voyage of Discovery to Terra Australis: by Willem De Vlamingh, 1696–97", after he discovered de Vlamingh's personal journal; this work was also reprinted. Phil was involved in the 400th anniversary celebrations of the landing of Dirk Hartog in Western Australia and jointly edited "The life and times of Dirk Hartog" published by the Royal Western Australian Historical Society in 2016. These interests also led to several public lectures and articles, the chairing of committees promoting aspects of WA's pre-colonisation history, and the installation of a replica of Dirk Hartog's plate on Dirk Hartog Island. Parts of the bulletins on the Devonian reef complexes and on Shark Bay were devoted to the history and Aboriginal heritage of the West Kimberley and the Shark Bay areas, respectively. In 1998 he was made a Member of the Order of Australia (AM) for 'contributions to geology and the history of early Dutch exploration and shipwrecks in Australia'. His life has truly been that of a renaissance man.

Phil is survived by his wife, Cynthia, children Julia and Katherine, and grandchildren James, Eloise, Laura and Max.

[Compiled by Tony Cockbain, Roger Hocking and Pam Reid from 'Biographical Notes' written by Phil Playford in May 2000].

Addendum by The Royal Society of Western Australia

As can be readily appreciated from the above, Phil has been generous with his involvement in organisations beyond those more work-related, one of these being The Royal Society of Western Australia. He first joined the Society in 1952 which in recent times must have made him one of its longest continuously involved members. He joined Council in 1965–66, became Vice President in 1967–69, and President in 1969–70 followed by a further year as the Immediate Past President 1970–71. Phil remained a Council member until 1984 then took a break until a second period of service between 1989–93. In 1999 he was given Honorary Life Membership of the Society and in 2001 awarded the Society's highest accolade, the Medal of The Royal Society of Western Australia. It was fitting and a reflection of his keen interest and concern that in 2014, the Society's Centenary year, Phil should join the Centenary Sub-committee to assist plan and guide the range of events undertaken to celebrate this significant milestone. It will be many years before we will see his like again; Council and members are most grateful for Phillip Playford's service to the Society and the pursuit of science in Western Australia.

[Compiled by William Loneragan, Lynne Milne and Greg Benjamin].

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Vale Professor Arthur McComb

BSc, MSc (Melb.), PhD (Cantab), DSc (Murdoch), F. Inst. Biol., FAA

9th December 1936–8th October 2017

Many members of the Royal Society of Western Australia were saddened to learn of the passing of Professor Arthur McComb. Arthur had a long association with the Society, joining in 1963, joint Secretary 1967–68, Editor of the journal from 1971–1976, Vice President 1977 and President in 1978. He was awarded the Kelvin Medal of the Royal Society of Western Australia in 1997.

Emeritus Professor Arthur McComb, Murdoch University, was an outstanding well-regarded Australian environmental scientist. He had a long and distinguished career in the field, contributing to marine, estuarine and freshwater science at a high level of scholarship and productivity. Arthur consistently applied his scientific expertise to the practical application of improving environmental management. He was passionate in wanting to improve the state of environmental management, based on rational, logical and well-founded biological principles. His research approach also provided the essential modelling capability to set management targets for nutrient reduction at whole ecosystem scale, in which WA has become a world leader in aquatic systems management.

Arthur McComb was born in Melbourne, on 9th December 1936, and graduated with a BSc and MSc from the University of Melbourne in 1959. He undertook his PhD at the University of Cambridge, graduating in 1962, and returned to Australia with a 1935 Rolls Royce. Arthur embarked on an academic life, first at The University of Western Australia (1963–1988) and subsequently as Professor at Murdoch University (1989–1996).

At the UWA Botany Department, Arthur met Jennifer Chessell, whom he married in 1966. One of Arthur's first ecological publications in this journal came early in his time at UWA, when he collaborated with Jen, documenting the wetland vegetation of Loch McNess, in Yanchep National Park. Jen reminisced that it is not hard for a relationship to last more than 50 years if it can survive the mud, blister bush, mosquitos and snakes of the Yanchep fens. Their son David was born in Perth in 1974 and daughter Christine in Leicester in 1976. In 2015, David and his wife Jennie produced a grandson, Nils. A succession of family dogs, Arthur's interests in music, history, gardening, and carpentry as well as rebuilding and keeping the Rolls Royce running, rounded out a busy existence.

With a strong background in experimental plant physiology, Arthur was an expert on the control of plant growth in aquatic systems. While at first most of Arthur's research was concerned with the control of plant growth, with emphasis on plant physiology in the laboratory, he later worked with plants in the environment, broadening to ecosystem function.

In 1989 he was appointed Professor of Environmental Science at Murdoch University, and went on to expand Environmental Science there, cementing his role as a champion for environmental issues. He felt very much at home with Murdoch's ethos and, both there and at UWA, was a constant contributor to the efficient functioning of a modern university, certainly never shirking from yet another committee or the chance to promote issues he felt important.

Arthur supervised 34 PhD students, was author or co-author of nine books, 156 refereed papers and book chapters. His former students are spread throughout Australia and the world, in universities including four full professors both in Australia and Europe, in government departments and leading consulting firms, all confirming his influence on driving our understanding and management of marine, estuarine and freshwater systems.

In Western Australia, Arthur's ability to effectively chair committees as well as his scientific expertise were recognised by successive State governments. Arthur served as Chair of the National Parks and Nature Conservation Authority, and of the Lands and Forest Commission. Federally, he was a member of the Life Sciences Panel of the Cooperative Research Centres Committee.

Arthur was awarded the Hilary Jolly Award, Australian Society for Limnology in 1991, the Kelvin Medal of the Royal Society of Western Australia in 1997, the Prime Minister's Centennial Medal for environmental science in 2001, the Australian Marine Science Association Silver Jubilee Award in 2002, and a DSc from Murdoch University in 2007. He was elected to the Australian Academy of Science in 1996, and was a Fellow of the UK Institute of Biology. Arthur was also honoured by the naming of an Upper Cretaceous ostracod, *Cytharopteron mccomborum*, by the late Professor John Neale, University of Hull.

Arthur in the laboratory in 1993 (Photo Brian Richards)

After retirement in 1996, Arthur continued to contribute to research at Murdoch through his appointment as Senior Scholar in Residence in Environmental Science. He also headed the Centre for Organic Waste Management. This seemed a strange transition but as he put it: 'When a large amount of organic material becomes available in the environment, much the same microbial processes are set in train, utilising the material as a source of energy and nutrients. This is regardless of whether that material be sewage sludge, lawn clippings, detritus in a seagrass meadow, beach wrack, the sediment surface in a wetland, or the gut of a dugong.'

He was always a generous collaborator and provided many opportunities for his post-doctoral fellows and postgraduate students, always willing to let someone "give it a go". I think he was fascinated to see where even the wildest idea would lead. Arthur said that the satisfaction he gained from seeing the application of his ecological research, and the interaction with the community meant more to him than the kudos of a paper in a leading journal.

Em Prof D. I. Walker in collaboration with
Em Prof J. A. McComb

School of Plant Biology

The University of Western Australia